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Correlation of the Abundance of Betaproteobacteria on Mineral Surfaces with Mineral Weathering in Forest Soils

C. Lepleux,[a,b] M. P. Turpault,[b] P. Oger,[c] P. Frey-Klett,[a] and S. Uroz[a,b]

INRA, UMR 1136 INRA Nancy Université Interactions Arbres Micro-organismes, Centre INRA de Nancy, Champenoux,[a] INRA UR 1138 Biogéochimie des Ecosystèmes Forestiers, Centre INRA de Nancy, Champenoux,[b] and Laboratoire de Géologie de Lyon, CNRS UMR 5276, Université de Lyon, ENS de Lyon, Lyon,[c] France

Pyrosequencing-based analysis of 16S rRNA gene sequences revealed a significant correlation between apatite dissolution and the abundance of betaproteobacteria on apatite surfaces, suggesting a role for the bacteria belonging to this phylum in mineral weathering. Notably, the cultivation-dependent approach demonstrated that the most efficient mineral-weathering bacteria belonged to the betaproteobacterial genus *Burhkolderia*.

Mineral weathering plays a central role in nutrient-poor environments such as temperate forest ecosystems developed on acidic soils. Indeed, beside the contribution of atmospheric deposits and recycling of chemical elements, soil minerals constitute the main reservoir of nutritive cations for the long-lasting functioning of forest ecosystems (2, 36, 53). In this context, the release of key nutritive cations by mineral weathering processes is crucial. It is now established that, in addition to purely abiotic processes, soil microorganisms affect ion cycling and plant nutrition by releasing nutritive cations from minerals (5, 10, 20, 21, 52).

In the last decade, minerals and more generally terrestrial and oceanic rocks have been investigated for the presence of microbial communities on their surfaces (5, 6, 7, 14, 23, 24, 25, 27, 44). Due to their nutritive value, minerals can be considered a true ecological habitat giving excellent physical support for the development of specific microbial communities (8, 11, 12, 21, 30, 43, 54). As an example, Gleeson et al. (21) demonstrated that the taxonomic structure of the bacterial communities colonizing granite minerals was not homogenous and varied in relation with the mineral crystals (muscovite, plagioclase, K-feldspar, and quartz) present in this granite. Our knowledge of the bacterial communities colonizing soil minerals, in contrast to those colonizing rocks, is very limited (13, 54). However, through the mineral-weathering process, soil minerals impact the bioavailability of nutritive cations in the soil, and the modifications of the concentrations of the nutritive cations due to weathering are expected to influence the taxonomic and functional diversity of the bacterial communities colonizing mineral surfaces compared to those of the surrounding bulk soil (13, 40, 54).

To date, the ability to weather minerals has been demonstrated for a large range of bacterial strains isolated from various environments such as the rhizosphere of several plants (10, 32, 39, 49) and granite samples from the Damma glacier (19, 30). This ability was notably reported for bacteria belonging to the *Arthrobacter*, *Bacillus*, *Burkholderia*, and *Collimonas* genera (3, 19, 33, 46, 51, 56, 57). Among these isolates, strains that belong to the betaproteobacterial genera *Burkholderia* and *Collimonas* and that were isolated from forest soil were characterized by higher mineral-weathering efficacy (31, 49, 51). Given the current absence of marker genes identified with mineral-weathering functions, these two bacterial genera and more especially their relative abundance have been proposed as bioindicators of bacterial weathering potential in forest soils (53). However, all these conclusions need to be confirmed for the mineral-associated bacterial communities in order to determine their mineral-weathering ability and their potential role in nutrient cycling in forest soils.

To investigate the bacterial communities colonizing and weathering minerals, pure and calibrated particles of apatite, one of the main accessory minerals encountered in Breuil-Chenue forest soil (34, 35, 41), were incubated in nylon bags for 4 years in the soil under five tree stands (beech [*Fagus sylvatica*], Norway spruce [*Picea abies*], Douglas fir [*Pseudotsuga menziesii* Franco], Corsican pine [*Pinus nigra* Arn. subsp. laricio Poiret var. *Corsicana*], and coppice with standards [CwS]). Due to protocol incompatibility and a low heterogeneity of bulk soil bacterial communities at the Breuil-Chenue site (52) (as determined by temporal temperature gradient gel electrophoresis [TTGE] [see Fig. S1 in the supplemental material]), a composite bulk soil (TBS) sample was generated. After 4 years, the dissolution level of these minerals was measured (1, 48). Genomic DNA (gDNA) was extracted from 250 mg of apatite particles or from the surrounding bulk soil using the PowerSoil DNA kit (MO BIO Laboratories, Inc.). Amplicon libraries targeting the V5-V6 hypervariable regions of the 16S rRNA gene were generated as described by Uroz et al. (52, 55). Pyrosequencing resulted in ca 230,000 reads which passed the length and quality criteria (16). MOTHUR was used to trim, denoise, and align the reads and to generate the operational taxonomic units (OTUs; 97% sequence similarity), as well as to perform the nonparametric analyses (45). Taxonomic affiliation was performed using MG-RAST (metagenome rapid annotation using subsystem technology) (37). For each tree stand, bacterial isolates were obtained from apatite surfaces and tested for their mineral-weathering abilities using a microplate bioassay as described by Uroz et al. (49). Biotite was used here instead of apatite as it was previously demonstrated that the same mineral-weathering bacterial strains efficiently weather a variety of minerals (2, 9, 25, 26, 50, 51). A portion of the 16S rRNA gene of each bacterial isolate was then

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Address correspondence to S. Uroz, uroz@nancy.inra.fr.
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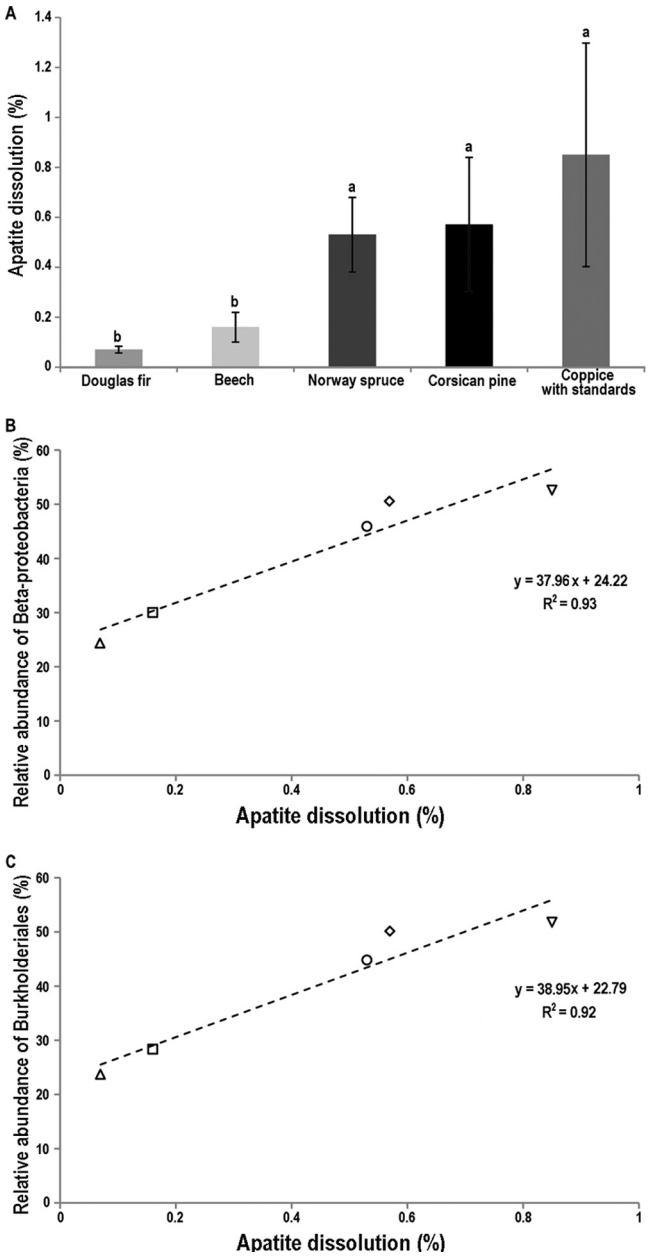

FIG 1 Apatite dissolution and relationship between the percentage of dissolution of apatite and the relative abundance of *Betaproteobacteria* and *Burkholderiales*. (A) Apatite dissolution. Bars represent the amount of apatite weight loss, i.e., the dissolution level, over the 4-year incubation period, expressed as percentages of the original weight. Bars associated with the same letters are not significantly different from each other according to a one-factor (tree species) ANOVA ($P = 0.0467$). (B) Relationship between the percentage of dissolution of apatite and the relative abundance of *Betaproteobacteria*. A positive and significant correlation between apatite dissolution and the abundance of 16S rRNA gene sequences assigned to the *Betaproteobacteria* class was found ($P = 0.0076$). (C) Relationship between the percentage of dissolution of apatite and the relative abundance of *Burkholderiales*. A positive and significant correlation between apatite dissolution and the abundance of 16S rRNA gene sequences assigned to the *Burkholderiales* family was found ($P = 0.0026$). The origins of the 16S rRNA gene sequences are indicated as follows: triangles, apatite below Douglas fir stand; squares, apatite below beech stand; circles, apatite below Norway spruce stand; diamonds, apatite below Corsican pine stand; inverted triangles, apatite below coppice with standards stand. The correlation between mineral dissolution and taxonomic classification or bacterial diversity was analyzed by performing a linear regression analysis at a threshold *P* value of 0.05 with the Statview software (SAS Institute, Cary, NC). The different relative values (%) used in this study were transformed by arcsine square root for statistical and linear regression analyses.

sequenced using the universal primers pA and 907r (17, 29). The abilities of the bacterial isolates coming from apatite surfaces to use single carbon sources were tested using Biolog GEN III microplates. The effects of the tree stand on mineral dissolution were determined by analysis of variance (ANOVA) at a threshold *P* value of 0.05 and by the Fischer test using the Superanova software (Abacus Concepts, Inc., Berkeley, CA). (For a complete description of the material and methods, see the supplemental material.)

After a 4-year incubation in the soils of the different tree stands, the most intensively weathered apatite particles were recovered from the coppice with standards (percentage of dissolution, 0.85% ± 0.4%), while the least-weathered particles were recovered from the Douglas stand (0.07% ± 0.01%). The apatite particles recovered from the coppice with standards, Corsican pine, and Norway spruce stands were significantly more weathered than those recovered from the beech and Douglas stands, according to a one-factor ANOVA (tree species) test ($P = 0.0467$) (Fig. 1A). One hypothesis to explain these differences is that the tree species differentially impact soil minerals through geochemical modifications of the soil conditions (e.g., pH) (1). However, the conclusions obtained considering the soil conditions (see Table S1 in the supplemental material) were not so clear, suggesting the influence of potential macro- and microscale conditions or microorganisms colonizing the mineral surfaces.

Nonparametric analyses revealed that, for similar numbers of sequences, the highest number of OTUs was observed for the bulk soil environment (13,557 OTUs) (see Table S2 in the supplemental material). Apatite surfaces were characterized by fewer OTUs, ranging from 8,323 to 10,071 OTUs under the different stands, with the exception of Corsican pine, for which only 3,798 OTUs were observed. Similar curves were obtained for the apatite sampled in the different tree stands, except under Corsican pine, which showed the lowest complexity (see Fig. S2 in the supplemental material). The nonparametric estimators ACE, Chao1, and Shannon revealed the same trend (see Table S2 in the supplemental material).

Classification of the sequences demonstrated that the same 19 phyla were present in all the samples considered, among which 4 were numerically dominant, i.e., *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, and *Bacteroidetes*. The bulk soil environment was dominated by *Proteobacteria* (53%) and *Acidobacteria* (8.50%). The apatite surfaces under each tree stand considered were dominated by *Proteobacteria* (49.75% under the Douglas fir stand to 73.05% under the coppice with standards stand), *Bacteroidetes* (7.03% under the coppice with standards stand to 36.97% under the Corsican pine stand), and *Acidobacteria* (0.55% under the Corsican pine stand to 15.89% under the Douglas fir stand) (Fig. 2). A detailed analysis revealed that the proteobacteria were dominated by alphaproteobacteria in the bulk soil (29.02%) and by betaproteobacteria on the apatite surfaces (24.82 to 52.65%) (Fig. 2).

At the genus level, apatite surfaces appeared dominated by *Burkholderia* (12.8 to 37.6%), *Pedobacter* (4.5 to 16.4%), and *Chitinophaga* (2.8 to 12.6%), with the exception of the coppice with

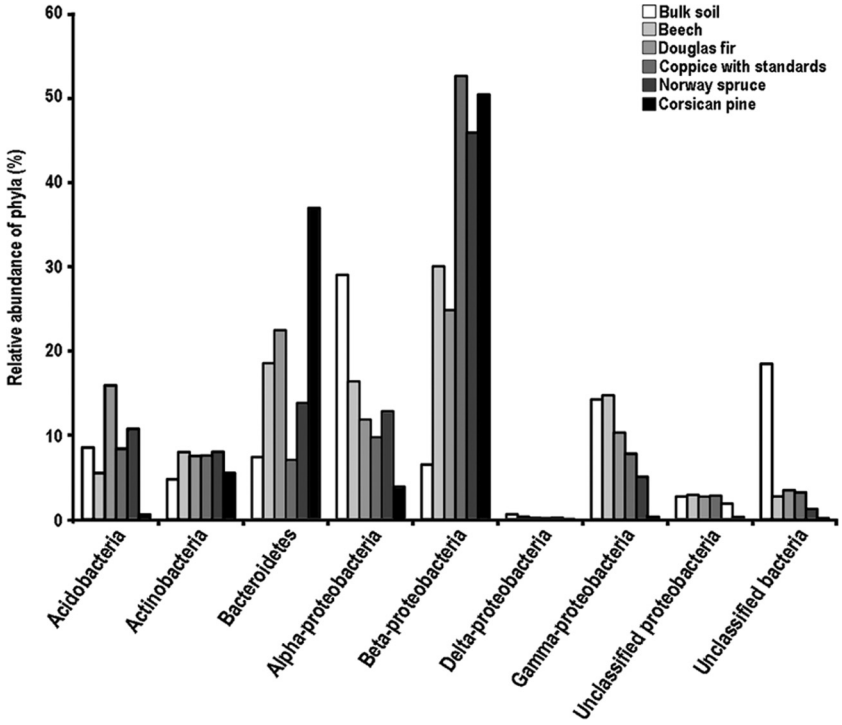

FIG 2 Relative abundances of the 9 most abundant phyla present at the apatite surface and in the surrounding bulk soil.

standards environment, where a predominance of sequences related to the betaproteobacteria from the *Oxalobacteraceae* family (*Herbaspirillum*, *Janthinobacterium*, and *Collimonas*; 16.11%) was observed (see Table S3 in the supplemental material). Only 1.60% of sequences related to the genus *Burkholderia* were recovered from the bulk soil, which was dominated by unclassified bacteria (ca. 13%). The relative distribution of phylotypes further differentiated the bulk soil and the mineralosphere. Among the 10 most abundant phylotypes detected on apatite surfaces, most belonged to the *Burkholderia* or *Collimonas* genus, known for mineral-weathering efficacy (9, 15, 33, 49, 51, 56, 57) (Table 1). Interestingly, the same *Burkholderia* phylotype (Table 1) was the major phylotype occurring in all stands, but not the coppice with standards environment, where it ranked 12th.

Notably, two positive and significant correlations between the level of apatite dissolution and the abundance of 16S rRNA gene sequences assigned to the *Betaproteobacteria* class or to the *Burkholderiales* order were found (Fig. 1B and C). Moreover, a significant correlation was observed for the *Burkholderia* genus when the data from the coppice with standards stand were omitted from

TABLE 1 Relative abundance of the 10 most abundant phylotypes[a]

Abundance ranking	Bacterium(a) to which phylotypes belong found in:					
	Bulk soil	Beech stand soil	Douglas fir stand soil	Coppice with standards stand soil	Norway spruce stand soil	Corsican pine stand soil
1	*Acidobacteria* bacterium	*Burkholderia**	*Burkholderia**	*Collimonas*	*Burkholderia**	*Burkholderia**
2	*Acidobacteria* bacterium	*Curtobacterium*	*Burkholderia*	*Collimonas*	*Burkholderia*	*Burkholderia*
3	*Acidobacteria* bacterium	*Dokdonella*	*Burkholderia*	*Collimonas*	*Burkholderia*	*Sphingobacteriaceae* bacterium
4	*Acidobacteria* bacterium	*Curtobacterium*	*Burkholderia*	*Collimonas*	*Burkholderia*	*Burkholderia*
5	*Bradyrhizobium*	*Mesorhizobium*	*Burkholderia*	*Oxalicibacterium*	*Streptomyces*	*Sphingobacteriaceae* bacterium
6	*Bradyrhizobium*	*Burkholderia*	*Burkholderia*	*Variovorax*	*Burkholderia*	*Burkholderia*
7	*Steroidobacter*	*Verrucomicrobia*	*Bradyrhizobium*	*Sphgobacteriaceae* bacterium	*Burkholderia*	*Sphingobacteriaceae* bacterium
8	Gammaproteobacterium	*Burkholderia*	*Burkholderia*	*Sphingobacteriaceae* bacterium	*Streptomyces*	*Sphingobacteriaceae* bacterium
9	*Paenibacillus*	*Sphingobacteriaceae* bacterium	*Burkholderia*	*Oxalicibacterium*	*Burkholderia*	*Burkholderia*
10	*Paenibacillus*	*Dokdonella*	*Burkholderia*	*Variovorax*	*Burkholderia*	*Burkholderia*

[a] Analyses were performed at a 97% sequence similarity threshold and calculated using the MOTHUR software. Asterisks indicate the presence of the same phylotype (100% sequence similarity) of *Burkholderia* on apatite surfaces.

the analysis (data not shown). Santelli et al. (44) also reported that, in another environment, the abundance of bacteria was positively correlated with the mineral-weathering levels, the oldest and most weathered basaltic rocks harboring the highest microbial biomass, suggesting an impact on the mineralogy.

These observations should be taken with caution, since quantification and reproducibility of pyrosequencing results are still questioned. Indeed several studies have illustrated some of the limits of the pyrosequencing approach in phylogenomic studies (22, 59). For example, Zhou et al. (59) showed low reproducibility in technical and biological replicates from a mixed-grass prairie soil, demonstrating a net decrease of the shared OTUs between replicates when the number of replicates increases. Part of this heterogeneity is linked to the experimental procedure, including biases in gDNA preparation and PCR amplification, variable efficiency of barcoded primers, and pyrosequencing artifacts (6, 18, 47) or is attributed to sampling artifacts (52, 58). Altogether, these biases can lead to an artificial view of the distribution of the bacterial communities, and an overestimation of rare taxa (28). Regardless of these artifacts, several authors conclude that this approach is especially valid in two instances: when the overall diversity is low and when the targeted communities live in the same habitat. One last important issue is the validation of the 454 sequencing-based phylogenomic results, using complementary methods such as microarrays, quantitative PCR, and cultivation-dependent approaches. In the present study, our phylogenomic results on the structure of the mineral-associated bacterial communities characterized by a low genetic diversity were obtained by pyrosequencing from a single pyrosequencing run. The results of the present study confirm and extend previous results obtained by cloning and Sanger sequencing of the 16S rRNA from the bacteria on the same minerals at the same forest experimental site (54).

The culture approach revealed that the bacterial isolates collected under the Douglas fir (mean value, 0.56 ± 0.10 mg · liter^{-1} of iron released) and Corsican pine (mean value, 0.46 ± 0.10 mg · liter^{-1} of iron released) stands were significantly more efficient at weathering ($P = 0.0001$) than those from the other environments (see Fig. S3 in the supplemental material). In addition, the apatite surfaces below Douglas fir and Corsican pine harbored a significantly higher frequency of the most efficient mineral-weathering bacterial isolates ($\geq$0.5 mg · liter^{-1} of iron released) than the other stands, according to a χ^2 analysis ($P = 0.0069$) (see Fig. S3 in the supplemental material). Taxonomic assignments of these isolates revealed sequences related to genera exhibiting high similarity with the 16S rRNA sequences generated by pyrosequencing in this study. A comparison of the mineral-weathering efficacies measured for each bacterial genus showed that the *Burkholderia* strains were the most efficient at weathering minerals (average value: 0.93 ± 0.14 mg · liter^{-1} Fe released), according to a one-factor (genus) ANOVA ($P = 0.0001$) (Fig. 3). The most efficient strain of *Burkholderia* (strain PA10) presented an *in vitro* mineral-weathering efficacy of 1.51 mg · liter^{-1} Fe released from biotite. The other genera presented values ranging from 0 (for *Cohnella* and *Cytophaga*) to 0.95 (for *Arthrobacter*) mg · liter^{-1} Fe released. Detailed analysis of the metabolic capability of the mineralosphere bacterial isolates in relation to their ecological origin (tree stand) revealed a very limited number of substrates metabolized and significant differences among the substrates metabolized by the mineralosphere bacteria below each tree stand (see Fig. S4 in the supplemental material). Our Biolog data indicated that there was no

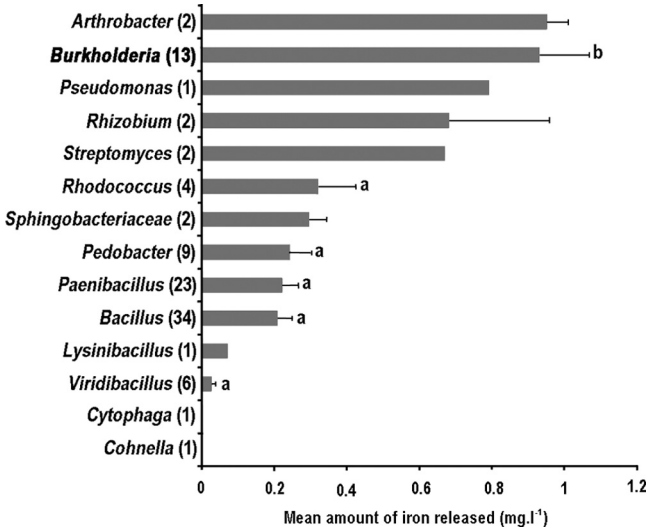

FIG 3 Relationships between the mean amount of iron released and the genus level classification of the bacterial strains. A total of 100 bacterial isolates were identified based on their 16S rRNA gene sequences and tested for their ability to weather minerals. The numbers of bacterial strains isolated per genus are in parentheses. For the genera with a minimum of three bacterial strains identified, a one-factor (genus) ANOVA was performed ($P = 0.0001$). Bars associated with the same letters are not significantly different.

significant difference in α-D-glucose consumption between the different tree stands (one-factor ANOVA [tree species]; $P = 0.12$) but that there were differences between the different bacterial genera. The bacterial isolates belonging to the *Burkholderia* genus consumed significantly more α-D-glucose (one-factor ANOVA [genus]; $P = 0.0001$).

In conclusion, this study demonstrates for the first time, by combining cultivation-dependent and -independent approaches, that mineral surfaces in forest soils are colonized by specific bacterial communities capable of mineral weathering, thus confirming the mineralosphere concept (51). In this view, although there may remain some uncertainty about their exact proportion on the mineral, there is little doubt that betaproteobacteria, and especially bacteria from the genus *Burkholderia*, are key players in the weathering of minerals and nutrient cycling in temperate forest soils.

Accession numbers. The 454 sequences generated have been deposited on MG-RAST under the following accession numbers: 4445487.3, coppice with standards; 4445488.3, Corsican pine; 4445489.3, Norway spruce; 4445491.3, beech; 4445490.3, Douglas fir; and 4445492.3, bulk soil. The sequences of the bacterial isolates have been deposited in the GenBank database under accession numbers JN819556 to JN819658.

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